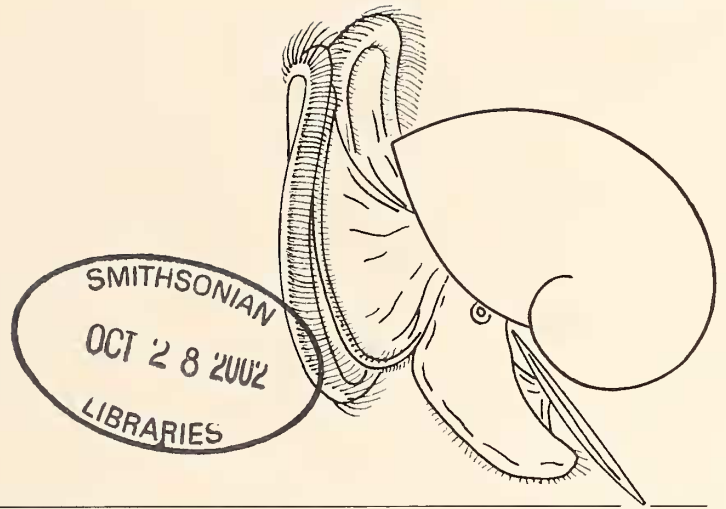


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VELIGER



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Very short papers, generally not over 750 words, will be published in a "Notes, Information & News" column; in this column will also appear notices of meetings and other items of interest to our members and subscribers.

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Movement and Wave Dislodgment of Mussels on a Wave-Exposed Rocky Shore

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Abstract. Postlarval dispersal of mussels has the potential to greatly influence the dynamics of mussel assemblages on rocky shores. We individually tagged mussels (*Mytilus trossulus* Gould, *M. edulis* Linnaeus) in situ to compare rates of movement and loss between habitats (tidepools, emergent rock), positions (inside, outside of patches), and seasons. Between 7% and 86% of tagged individuals (5–25 mm shell length) moved ≥ 1 cm within 2–4 week intervals. Rates of movement were greater in July, when wave forces are lower, than in October, and were greater for mussels outside of patches than for those inside patches. Most tagged mussels moved distances of 1–2 cm, although 9% of movements were >10 cm. Many of the tagged mussels disappeared over the course of the 3–4 week monitoring intervals, most likely due to wave dislodgment. The frequency of mussel disappearance was generally similar inside and outside of patches and between habitats, with the exception of a higher disappearance rate in October than July 1995 for mussels in tidepools but not on emergent rock. This study demonstrates that mussel patches on a wave-exposed shore are dynamic, with movements constantly rearranging individuals within patches, and high rates of loss of individuals, presumably from wave disturbance.

INTRODUCTION

Mussels form patches or large beds on rocky shores, and often are major occupiers of space in the intertidal zone (Seed & Suchanek, 1992). Although mussels generally are thought of as sessile, they are not permanently attached to the substratum. Young postlarval mussels can use byssal threads that increase hydrodynamic drag to drift in the water column (Sigurdsson et al., 1976; De Blok & Tan-Maas, 1977). Larger juvenile and adult mussels may disperse actively over short distances by crawling, or passively over greater distances by wave dislodgment.

Active dispersal by crawling generally has not been considered important in prior studies of intertidal mussel assemblages, although *Mytilus edulis* Linnaeus, 1758, within subtidal aggregations have been observed to constantly move and reorient themselves (Dolmer et al., 1994; Anthony & Svane, 1995). Mussels may be less mobile in the intertidal zone of wave-exposed shores, where they must attach firmly to the substratum to withstand wave forces, than in the subtidal zone. Nevertheless, even movements over small distances could greatly influence rates of growth and mortality if they change a mussel's location within a patch or result in movement to a new patch. Mussels living in the center of groups generally experience reduced growth, but greater protection from

predation compared to individuals around the edge (Okamura, 1986). Living within an aggregation also shields mussels from hydrodynamic forces acting along the direction of flow (Denny, 1987) and is predicted to buffer individuals against rapid changes in temperature (Hel-muth, 1998). Studies have found a negative (Okamura, 1986; Newell, 1990; Svane & Ompi, 1993) or positive (Hunt & Scheibling, 2001a) relationship between mussel growth rate and patch size.

Larger displacements of adult mussels are likely to occur passively through dislodgment and redistribution by waves. Dislodgment by waves is a major cause of loss of mussels in the intertidal zone (e.g., Paine & Levin, 1981). Although some of the mussels dislodged by waves undoubtedly die, others probably are redistributed to new patches. Adult mussels have been observed colonizing cleared areas on rocky shores (Paine, 1974; Wootton, 1993). At our study site in Nova Scotia, we found that most mussel colonists were >2 mm in shell length (Hunt & Scheibling, 1998b). Also, the greatest changes in mussel patch size usually occurred suddenly and often were associated with storms, suggesting that large mussels were dislodged and re-deposited by waves (Hunt & Scheibling, 2001a).

In this study, we quantified rates of movement and disappearance of tagged mussels on a wave-exposed shore in Nova Scotia, Canada. Rates of movement were compared between habitats (tidepools and emergent rock), positions (inside and outside of patches), seasons (summer and fall), and years. Mussels were tagged in situ to avoid disturbance of their attachment to the substratum.

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METHODS

This study was conducted on an exposed rocky shore at Cranberry Cove (44°28'N, 63°56'W) near Halifax, Nova Scotia, Canada. The shore is composed of granite platforms and outcrops with occasional large boulders. There are numerous tidepools in irregular depressions along the shore, ranging from a few decimeters to over 10 m in maximum dimension. The shore is exposed to large southerly swells during fall and winter storms. Mussel assemblages at Cranberry Cove consist of a mixture of *Mytilus trossulus* Gould, 1850, and *M. edulis*: approximately 65–80% of mussels in tidepools and on emergent rock are *M. trossulus*, the remainder consist of *M. edulis* and hybrids of the two species (Hunt & Scheibling, 1998b). *M. trossulus* and *M. edulis* cannot be distinguished visually at the small size of the individuals at our study site. Most mussels are < 5 mm in shell length (SL); very few exceed > 20 mm (Hunt & Scheibling, 1998a).

We investigated the mobility of mussels by tagging individuals ~ 5 to 25 mm in shell length with numbered plastic bee tags (Steele & Brodie Ltd., Hampshire, England). These tags are small (2.6 mm diameter, 0.02 mm thickness) and lightweight (0.0014 g) and presumably have no measurable effect on movement of mussels. The same tags have been used to study swimming movements of juvenile scallops within a similar size range (Carsen et al., 1995). In August 1994, we tagged 15 individuals in each of two tidepools and two plots of emergent rock and monitored them for 2–3 weeks. In July and October 1995, we tagged 20 mussels in both a tidepool and an adjacent plot of emergent rock and monitored them for ~ 4 weeks.

The mussels were tagged in situ after temporarily draining the water from the tidepools. We dried one shell valve on each selected mussel, cleaned it with acetone, and affixed a tag using cyanoacrylate glue. Mussels < 5 mm were not tagged because their small size made it difficult to attach a tag without gluing the valves shut. Tagged mussels were grouped into two categories of initial position: in natural patches (at center or edge) and outside of them (alone or in a small group, or on top of the single layer of mussels in a patch). Mussels on top of a patch were considered to be outside because their frequencies of movement and disappearance were more similar to those of solitary mussels than to those in patches. We determined the location of each tagged mussel at 2–10 day intervals by measuring the distances between the mussel and two reference bolts drilled into the rock. We converted these distances to x and y coordinates and trigonometrically calculated the distance moved by a mussel between sampling dates from the coordinates for each date. These distances are minimum values, since mussels could have moved nonlinearly between sampling dates. We compared distances of movement between habitats, positions, and dates using ANOVA or t-tests, and the fre-

quencies of movement and disappearance of mussels using contingency tables (G-test).

RESULTS

The tagged mussels were mobile, although they moved infrequently and for short distances. In August 1994 and July 1995, 21 to 56% of mussels in patches and 67 to 86% of those outside of patches moved within 13–27 days (Figure 1). In October 1995, only 7–10% of mussels in patches and 43–66% of isolated mussels moved within 30 days (Figure 1). The percentage of mussels that moved did not differ significantly between tidepools and emergent rock during each monitoring interval (August 1994: in patches, $G_1 = 2.87$, $P = 0.09$; outside, $G_1 = 0.27$, $P = 0.60$; July 1995: in patches, $G_1 = 1.44$, $P = 0.23$; outside, $G_1 = 0.07$, $P = 0.79$; October 1995: in patches, $G_1 = 0.11$, $P = 0.74$; outside, $G_1 = 0.56$, $P = 0.46$). Mussels outside of patches in both habitats were significantly more likely to move than those in patches (habitats pooled; August 1994, $G_1 = 6.66$, $P = 0.01$; July 1995, $G_1 = 10.48$, $P = 0.001$; October 1995, $G_1 = 11.49$, $P = 0.001$). In 1995, a higher percentage of mussels in patches moved in July than in October (habitats pooled, $G_1 = 4.93$, $P = 0.03$), when wave heights were much greater (Hunt & Scheibling 2001b). The percentage of mussels outside of patches that moved did not differ significantly between these dates (habitats pooled, $G_1 = 1.16$, $P = 0.28$).

Distances moved by tagged mussels were usually < 5 cm with a modal class of 1–2 cm, although six out of 68 individuals moved 10–49 cm (Figure 2). Distance moved during August 1994 and July 1995 did not differ significantly between tidepools and emergent rock (August 1994, pooled across plots: $F_{1,22} = 1.20$, $P = 0.29$; July 1995, $F_{1,26} = 0.84$, $P = 0.37$; October 1995, outside mussels (there was insufficient data to include mussels in patches in the analysis): $t_7 = 0.49$, $P = 0.64$), or between mussels in patches and those outside (August 1994: $F_{1,22} = 0.009$, $P = 0.93$; July 1995, $F_{1,26} = 0.008$, $P = 0.93$), and there was no significant interaction between habitat and position (August 1994: $F_{1,22} = 0.93$, $P = 0.35$; July 1995: $F_{1,26} = 0.37$, $P = 0.55$).

During each of the monitoring intervals, some tagged mussels were not relocated. These mussels probably were dislodged by waves and moved beyond our limited survey range of ~ 50 cm radius around their initial location. These disappearances were unlikely to have been tag losses because some tags from 1994 were still visible in 1995. Disappearances also were unlikely to have resulted from predation. Mussels eaten by the whelk *Nucella lapillus*, the only abundant predator of mussels at this site (Hunt & Scheibling, 1998a, 2001a), remained attached to the substratum and were identified by the presence of a drill hole. We have occasionally observed crabs at Cran-

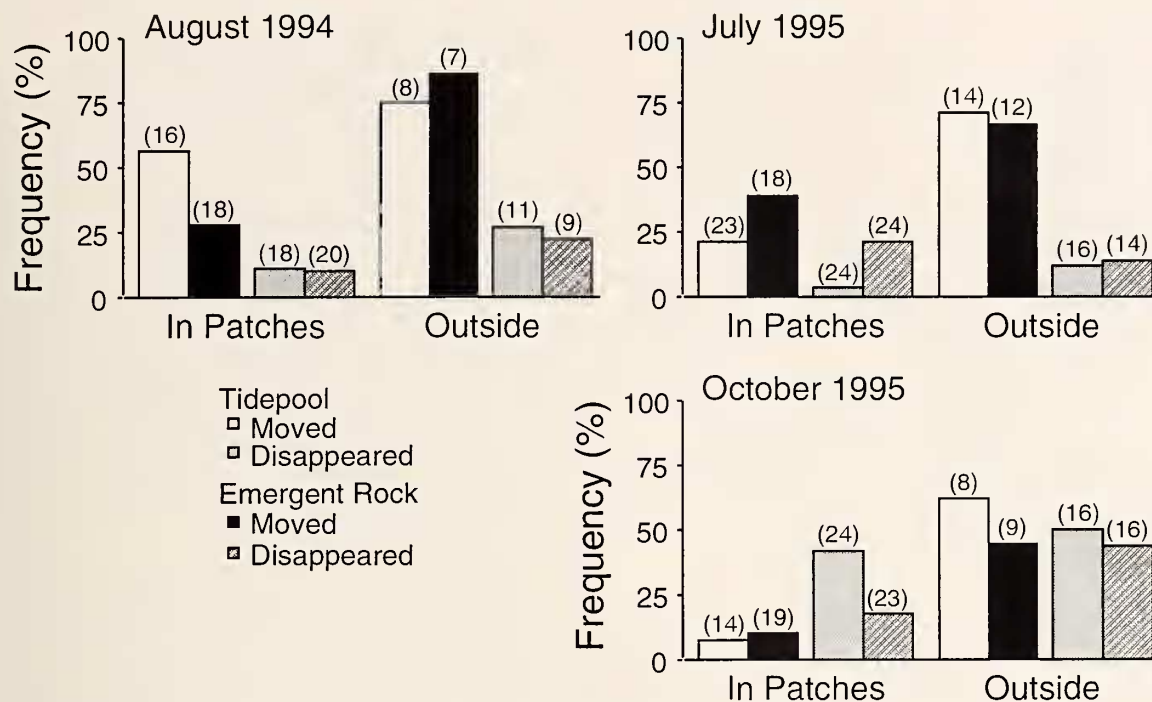


Figure 1. Frequency (%) of movement and disappearance of tagged mussels in patches and those outside of them (alone or in small group, or on top of the single layer of mussels in a patch) in tidepools and on emergent rock in August 1994 (pooled across plots within a habitat) and July and October 1995. Frequency of movement was calculated as a percentage of the mussels that were tracked throughout a monitoring interval. Frequency of disappearance was calculated as a percentage of the total number of tagged mussels. Sample size is indicated in parentheses.

berry Cove, but have found little evidence of crushed mussel shells indicative of crab predation.

In August 1994 and July 1995, 10–22% of mussels in patches and 13–27% of those outside of patches disappeared (Figure 1). In October 1995, when wave heights were greater, 42% and 17% of mussels in patches in tidepools and on emergent rock, respectively, and 44–50% of mussels outside of patches in both habitats, disappeared (Figure 1). The frequency of disappearance of mussels in July 1994 and August 1995 was too low to permit statistical comparisons of disappearance rate between habitats and positions. In October 1995, the frequency of disappearance did not differ significantly between tidepools and emergent rock, both for mussels in patches, ($G_1 = 3.40$, $P = 0.065$), and for those outside of patches ($G_1 = 0.13$, $P = 0.72$). The frequency of disappearance also did not differ significantly between mussels in patches and those outside (habitats pooled, $G_1 = 2.38$, $P = 0.12$). In 1995, the frequency of disappearance in tidepools was significantly greater in October than in July, both for mussels in patches ($G_1 = 10.8$, $P = 0.002$) and those outside ($G_1 = 6.5$, $P = 0.011$). In contrast, the frequency of mussel disappearance on emergent rock did not differ significantly between dates for mussels in patches ($G_1 = 0.14$, $P = 0.710$) and those outside ($G_1 = 3.2$, $P = 0.07$). These results indicate that the frequency

of mussel disappearance was generally similar in and outside of patches and between habitats, with the exception of a higher disappearance rate in October than July 1995 for mussels in tidepools but not on emergent rock.

DISCUSSION

It has long been recognized that *Mytilus edulis* detached from the substratum will crawl using their foot and byssal threads (e.g., Maas Geesteranus, 1942). However, most studies of mussels on hard substrates have recorded little mobility of undisturbed *Mytilus*. Our tagging study indicated that a significant proportion of mussels moved short distances. For example, 21–56% of mussels in patches in summer moved within 4 weeks. Some of these movements could have occurred by wave dislodgment rather than by crawling. In a study that examined mussels as a substrate for anemones, Anthony & Svane (1995) monitored movements of *M. edulis* in a subtidal mussel bed photographically. The frequency of movement of mussels in their study was higher (94% moved within 4 weeks) than in ours, possibly because lower water velocities in the subtidal permit mussels to be less strongly attached to the substratum. In contrast, Okamura (1986) found that *M. edulis* established in patches on tiles did not move from edge to central positions or vice versa. Paine (1974)